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THE SPAWNING HABITS OF CHROSOMUS ERY- THROGASTER RAFINESQUE.*

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While a student at the University of Michigan during the years 1904-1907 I acted as assistant in zoölogy and when accompanying Professor Jacob Reighard on field excursions had many opportunities to observe, under his guidance, the breeding habits of minnows and other fishes. This familiarity with the unpublished work of Professor Reighard made it possible for me to make the observations recorded below, which are published with his permission.

About the middle of May, 1907, I found the minnow *Chrosomus erythrogaster* Rafinesque very abundant in a small brook near Lake Forest, Ill. As the males were in breeding dress I seized the opportunity to make some observations on the spawning habits.

Habitat.—The brook flows through a large open pasture and also through woodland; the minnows were far more numerous in that portion of the brook which is in the open field. Here the stream meanders through a shallow valley, over a pebbly or sandy bottom. In places it is so narrow that one can readily step across it; elsewhere it expands into pools or shallow rapids not more than six feet wide. In the rapids the water is seldom more than two or three inches deep; in the pools it may reach a depth of one or two feet. The current is quite rapid; even in the pools there is little quiet water.

Chrosomus is by far the most abundant fish in this brook. Schools of from a dozen to several hundreds abound, while of other fishes only a few large suckers, and an occasional *Rhinichthys*, *Semotilus* and *Cottus*, were observed.

Sexual Dimorphism.—The bright colors of the males were scarcely noticeable when the fishes were in the water and viewed obliquely from above; but when removed from the water the

* Contributions from the Zoölogical Laboratory of Syracuse University.

males were found to be marked on each side of the abdomen with a broad longitudinal stripe of the most vivid and brilliant scarlet that I have ever seen. This stripe starts just back of the operculum and runs immediately below the lower of the two lateral dark bands (see Fig. 1) and parallel to it, reaching almost to the caudal fin. There is also a small red spot just below the

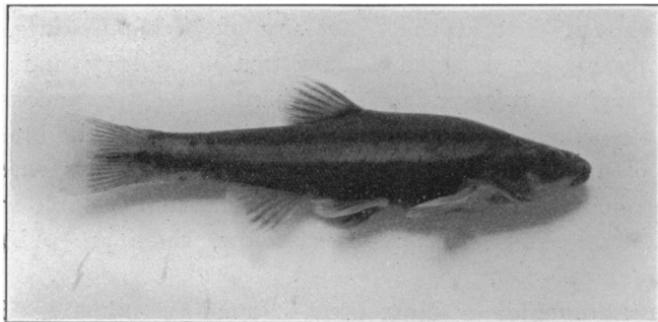


FIG. 1.



FIG. 2.

FIG. 1, male, and Fig. 2, female specimens of *Chrosomus erythrogaster* Rafinesque, life size.

mandible on each side. In some specimens the lateral bands of red are faint except just behind the operculum. In the more highly colored males the entire abdomen is covered with red, and there is a red spot in the anterior part of the root of the dorsal fin. The pectoral and pelvic fins, and the anal fin, are bright lemon yellow; the dorsal fin and tail are faintly marked with pale yellow. There is a small spot of yellow on the ventral side of the body at the base of the caudal fin, and another in the gular region.

The males possess "pearl organs" (small conical thickenings of the epidermis), occurring over practically the entire surface of the body, head, tail and fins. They are especially numerous and well developed on the dorsal and lateral surfaces of the body, on the opercula, over the entire surface of the tail, and on the dorsal surfaces of the pectoral fins; they are large, but comparatively few in number, on the dorsal surface of the head. They are much smaller on the ventral surface of the abdomen, and entirely lacking about the mouth and at the tips of the fins.

As seen under the microscope, a pearl organ from the body of a male is a sharply pointed transparent spine, rising from a broad base and pointing obliquely backward, occurring as a thickening of the epidermis over the middle of the posterior margin of each scale. Usually there is only a single pearl organ for each scale, but sometimes two spines occur close together. Smaller rudimentary pearl organs, each consisting of a papilla or thickening of the epidermis without a spine, also occur, one or more over each scale and usually near its center.

The pectoral fins of the male are much larger and stronger, in proportion to size of body, than those of the female. As shown by average measurements, the pelvic fins of the male are also proportionally larger than those of the female, but the difference is not so great as in the case of the pectoral fins.

The females are on the average slightly smaller than the males (see Figs. 1 and 2), but have the abdomen distinctly swollen. There is a small patch of red just back of the operculum. They have the same yellow coloration as the males, but the color is comparatively faint. They possess only rudimentary pearl organs, hardly visible except under the microscope.

A notable exception to the usual sexual dimorphism was found in the case of one unusually large female with well developed ovaries and eggs, but with the secondary sexual characteristics of the male all very well marked.

I had no opportunity to study the color changes and the history of the pearl organs throughout the year.

Sex Ratio.—In order to determine the numerical proportion of the sexes, representative samples of several schools were taken on several different days. The tabulated results are as follows:

Date of Capture.	Mode of Capture.	Number in Catch.	Females.	Males	Ratio.
1. May 17.....	Hoop net	6	2	4	1 : 2
2. " 29.....	Single sweep of seine	119	9	110	1 : 12.2
3. " 31.....	Hoop net	80	14	66	1 : 4.7
4. June 14.....	Hoop net	15	4	11	1 : 2.7
	Total..	220	29	191	1 : 6.5

In lots 1, 3 and 4 the sexes were determined by dissection. Since in only one of these specimens the secondary sexual characters were those of the opposite sex, the probable error in determining the sex by the external characters is a negligible quantity. In lot 2 the sexes were determined by the external characters.

These results are sufficient to indicate a decided preponderance in the number of males on the spawning ground at the spawning season, though not necessarily at other times or places.

Spawning Behavior. — The casual observer will find schools of *Chrosomus* occurring in the pools and the deeper portions of the swift water of the brook. On quietly approaching the stream, one will often notice a splashing of the water of the shallow rapids, scarcely distinguishable from the ordinary rippling of the current. Further observation will reveal the fact that in places the water is alive with tiny fishes, struggling and crowding one another in water so shallow that the surface is violently agitated; occasionally a mass of wriggling fishes will flash into view at the very surface, or crowd splashing upon the pebbly shore, where some may be left stranded, later to struggle back into the water.

When alarmed, the fishes almost invariably swim up stream from the shallows. In the deeper water they gradually recover from their fright; those that have hidden amongst the water vegetation or under the shadow of overhanging banks, rejoin the school. Together, moving in unison like a flock of sheep, they surge slowly down stream; but before they reach the shallow water again, they face about with an eddying movement, and swim up stream. This circuit is made repeatedly, the school drifting each time a little farther down stream toward their proper spawning grounds. The behavior of the fishes from the time they are frightened away from the shallows, until they resume

active spawning operations on the same ground, forms a series of events which occur on different occasions with unfailing regularity.

On the up stream journey, occasional isolated cases of spawning occur. Several males pursue one female; as the foremost males gain a position alongside the female, the flight and pursuit attain almost lightning-like rapidity. At length two males spawn with the single female as follows: One on each side presses the side of his head against that of the female, all three facing up stream. The two males then crowd laterally against the female, held between them (see Fig. 3); their entire flanks are thus pressed against the sides of the female. While the males are in this position, a rapid vibration of their bodies occurs. The wave of pressure begins at the anterior end of the body and passes backward as a sidewise undulating movement. Other males may attempt to crowd in. So far as observed, the female remains passive. The entire performance occurs so quickly that the details are made out only after considerable practice in observation.

Spawning under these conditions seems to be attended with difficulty. The act of clasping lasts but for an instant; the males seem unable to keep their position after the impetus of their rush up stream is overcome by the current, for swimming movements are necessarily discontinued during spawning. It is doubtful if spawning in the open, without contact with the bottom, is very effective; milt was not extruded in sufficient quantities to be seen. Although the eggs (almost transparent, with light-brown yolk, always difficult to see in the water) could not be seen, it was evident that some were extruded, for immediately after the spawning other fishes poked their noses into crevices between pebbles, just down stream from where the spawning occurred, evidently trying to get at the scattered eggs to eat them.

As the school in its circling movements nears the shallows, a

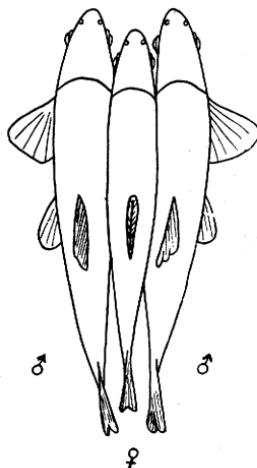


FIG. 3. *Chrosomus* in spawning position. Natural size.

few of the foremost fishes, with shy, frightened movements, dart rapidly down stream through the swift water of the regular spawning grounds ; after the first reconnaissance they hurry back to rejoin the main body, and the entire school moves up stream. This is repeated several times ; each time the band of more venturesome fishes is increased in number, and a little later, on the up-stream journey, they stop for a time to spawn on the pebbly margin of the stream. Soon the entire school, in a compact body, is spawning on the shallows. With their swift movements



FIG. 4. Spawning grounds of *Chrosomus*. The shallow water near shore is occupied by a school of several hundred *Chrosomus*; some of these may be indistinctly seen, in spawning position, at the surface of the water in the center of the picture.

and brilliant colors, this writhing mass of several hundred fishes affords a truly remarkable spectacle.

Persistent attempts to photograph the spawning operations met with poor success, a result due in part to the lack of a suitable camera. Figs. 4 and 5 are reproductions of two of the many views taken.

This procedure of spawning *en masse* in shallow swift water

may be regarded as the normal spawning behavior of these fishes. All the fishes face up stream, but their swimming movements are only sufficient to keep them from being swept down stream by the current. In the confused and wriggling mass it is difficult to distinguish the movements of individual fishes ; but it may be seen that many males crowd alongside a single female, and those immediately in contact with her may occasionally be seen in the spawning position described as occurring in the deep water.

Gradually the school crowds closer against the shore, rasping



FIG. 5. Spawning grounds of *Chrosomus*. Spawning fishes crowding up on the island of gravel, may be seen near the center of the picture. In the foreground the water is alive with fishes.

over the pebbles and wriggling into water so shallow that their dorsal surfaces are exposed. In these situations small groups become segregated from the main mass ; their progress is impeded by the pebbles, so that accurate observation becomes an easy matter. Typically, two males lie alongside a single female ; the group becomes wedged in between large pebbles and in close contact with the bottom, so that the males are enabled to keep

their position indefinitely, and lie for many minutes motionless except for the frequently occurring rapid vibration of their bodies. The spawning position is exactly the same as that observed in the open, but the performance is greatly prolonged, and spawning doubtless much more effective. Frequently, groups of four or even more fishes were seen lying alongside, with their bodies in close contact ; occasionally a group of six, composed of two trios, each consisting of a single female, spawning with two males.

One marked variation from the usual spawning method was observed. A female in very shallow water spawned with a single male, which crowded her laterally against some pebbles and curved his tail up over her body, thus holding her firmly against the bottom. His body vibrated rapidly and the water became cloudy with milt.

Some further observations on the spawning behavior were obtained by the study of a small school which occupied an abandoned dace's nest. When first observed, this school consisted of a dozen or more males, crowded closely together in the hollow of the nest. Occasional females approached shyly from down stream, singly, or two or three in succession ; sometimes darting rapidly, as if excited or frightened, up the middle of the stream ; again keeping close to the shore, and occasionally seeking cover. The arrival of a female created intense excitement amongst the males in the nest. They immediately crowded around her, pressing alongside and against her in the hollow of the nest. After spawning, the males devoted considerable attention to prying about between the pebbles as if searching for eggs. Sometimes the males, in a body, left the nest and returned to it repeatedly, moving in an excited manner as if seeking to entice or drive a female into it. The nest was evidently an especially favorable place for spawning.

Eggs in various stages of development were obtained by scooping up the gravel of any of the spawning grounds.

Breeding Season. — The earliest observations were made on May 17. At this time the bright colors of the males were well developed and spawning was in progress, but how long it had been going on is not known. The latest observations were made on June 14 ; then the schools of fishes spawning on the shallows

were small, while in the pools below were larger schools which took no interest in spawning, and were comparatively inactive. The males of these latter schools had nearly lost their bright colors. Evidently the breeding season was nearly over. At this time many of the eggs had hatched out.

During this prolonged breeding season, extending over fully a month, the stream was frequently swollen by freshets, which presumably interfered with the spawning operations.

Discussion. — As shown by the unison of their circling movements when not engaged in spawning, and by the fact that they occur in schools even after the spawning season is over, these fishes possess a strong gregarious instinct. The two conspicuous longitudinal dark stripes on the sides of the bodies of both sexes probably serve as recognition marks.

The distribution of pearl organs over practically the entire body of the male affords a roughened surface which during spawning aids him in keeping his position beside the female. The function of the pearl organs of the Cyprinidæ was first discovered and described by Reighard ('03). The structure of pearl organs has been figured by various writers.

The greater size and strength of the pectoral fins of the male as compared with the female, and the fact that the dorsal surfaces of these fins are unusually well provided with pearl organs, indicate that these fins are of use to the male in holding the female. The male, coming up from the rear, doubtless interlocks his pectoral fin between the pectoral fin and the body of the female, though it was impossible to see this.

The excessive number of males present on the spawning grounds is perhaps correlated with the method of spawning, since two males spawn with a single female.

The observable factors in sex recognition are: the brilliant colors and aggressive bearing of the male; the dull colors, swollen abdomen, and timid, hesitating movements of the female.

It is significant, in its bearing on current theories of secondary sexual characteristics, that the female showing the secondary sexual characters of the male was an unusually large and apparently vigorous specimen; but it would be unwise to base conclusions on a single instance.

The total absence of combat amongst the males accords with the necessity for coöperation in the spawning act. Competition amongst the males is limited to the struggle to get a position next to the female; in this contest the swiftest and strongest succeed.

In general the method of spawning is adapted to fishes with gregarious habits, and would seem hardly likely to be developed amongst fishes whose usual habit of life is solitary.

The pebbles amongst which the eggs lodge afford them some protection, though it appears that some of the eggs are eaten by the parent fishes. The gradual subsidence of the water during the latter part of the season must have left some of the eggs to perish on the shore. That the method of spawning is, in general, a successful one is attested by the abundance of these fishes in this brook.

A comparison with the habits of other inland fishes would be impossible without reference to the unpublished work of Professor Jacob Reighard.

SYRACUSE UNIVERSITY,
April, 1908.

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